

# Asexual Reproduction in *Pygospio elegans* Claparède (Annelida, Polychaeta) in Relation to Parasitism by *Lepocreadium setiferoides* (Miller and Northup) (Platyhelminthes, Trematoda)

DEAN G. McCURDY\*

*Coastal Studies Center, 6775 College Station, Bowdoin College, Brunswick, Maine 04011-8465*

**Abstract.** Life-history theory predicts that parasitized hosts should alter their investment in reproduction in ways that maximize host reproductive success. I examined the timing of asexual reproduction (fragmentation and regeneration) in the polychaete annelid *Pygospio elegans* experimentally exposed to cercariae of the trematode *Lepocreadium setiferoides*. Consistent with adaptive host response, polychaetes that became infected by metacercariae of trematodes fragmented sooner than unexposed controls. Parasites were not directly associated with fission in that exposed polychaetes that did not become infected also fragmented earlier than controls. For specimens of *P. elegans* that were not exposed to trematodes, new fragments that contained original heads were larger than those that contained original tails, whereas original head and tail fragments did not differ in size for infected polychaetes. In infected specimens, metacercariae were equally represented in original head and tail fragments and were more likely to be found in whichever fragment was larger. Despite early reproduction, parasitism was still costly because populations of *P. elegans* exposed to parasites were smaller than controls when measured 8 weeks later and because exposure to cercariae reduced survivorship of newly divided polychaetes. Taken together, my results suggest that early fragmentation is a host response to minimize costs associated with parasitism.

## Introduction

Hosts respond to parasitism in a number of ways, which include avoidance of parasites in space or time (*e.g.*, mi-

gration; Folstad *et al.*, 1991), removal of parasites before they cause damage (*e.g.*, grooming; Léonard *et al.*, 1999), and immunological defense (*e.g.*, encapsulation; Kraaijeveld and Godfray, 1997). There is increasing evidence that hosts may also exhibit life-history adaptations to minimize the impacts of parasites on reproductive success (Minchella and LoVerde, 1981; Polak and Starmer, 1998; McCurdy *et al.*, 1999, 2000a). Life-history responses of hosts after exposure to parasites represent reallocations of energy in ways that increase reproductive success relative to non-responses. This type of reaction has been termed an adaptive host response (Minchella, 1985; Forbes, 1993). Unlike avoidance or resistance to parasites, life-history responses pose little or no maintenance costs to hosts (*i.e.*, no cost when parasites are absent) because the hosts do not alter their life histories until they come into contact with parasites (Minchella, 1985). Specifically, in systems where parasites pose greater costs to host energy budgets over time (decreasing future reproductive potential to a greater extent than current reproduction), hosts are expected to respond to infections by hastening their onset of reproduction. This response occurs, for example, in intertidal amphipods infected by trematodes (McCurdy *et al.*, 1999, 2000a). Although the reproductive success of hosts that respond through life-history variation is lower than that of hosts not exposed to parasites, it is greater than that of infected hosts that fail to respond (McCurdy *et al.*, 2001).

To date, tests of the hypothesis of the adaptive host response have been confined to hosts that reproduce sexually (Minchella and LoVerde, 1981; Polak and Starmer, 1998; McCurdy *et al.*, 1999, 2000a). However, the responses of sexual hosts can be difficult to interpret because selection may act differently on males and females to max-

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\* Current address: Department of Biology, Albion College, Albion, Michigan 49224.

E-mail: dmcurdy@albion.edu

imize reproductive success (Zuk, 1990), and because of factors specific to sexual mating systems (e.g., mate availability and choice; McCurdy *et al.*, 2000b; but see Minchella and LoVerde, 1981, for an exception). As a result, host investment in reproduction (reproductive effort) is assessed, but the actual consequences of this investment (reproductive success) are difficult to quantify (Perrin *et al.*, 1996; McCurdy *et al.*, 2000a).

I tested for adaptive host response in an asexual spionid polychaete, *Pygospio elegans*. This species is common in intertidal mudflats and sandflats throughout the Northern Hemisphere (Anger, 1984). Adults of this species construct tubes in the sediment and feed on detritus and phytoplankton (Anger *et al.*, 1986). Asexual reproduction in *P. elegans* is accomplished through transverse fragmentation, followed by rapid regeneration of missing components (Rasmussen, 1953; Hobson and Green, 1968; Gibson and Harvey, 2000). Wilson (1985) found that asexual reproduction in *P. elegans* is density- and resource-dependent in that populations grew larger when polychaetes were housed at low densities or provided with augmented levels of food. The impacts of parasitism on asexual reproduction and regeneration, however, have not been investigated in this or other species of polychaetes.

I investigated life-history responses of *P. elegans* to parasitism by exposing polychaetes to cercariae of the trematode *Lepocreadium setiferoides*. During the spring and summer, cercariae emerge from mud snails, *Ilyanassa obsoleta*, and infect spionid polychaetes as second-intermediate hosts; winter flounder, *Pseudopleuronectes americanus*, serve as final hosts of the parasite (Martin, 1938; McCurdy *et al.*, 2000c). In their polychaete host, trematodes do not reproduce. However, unlike many species of trematodes that emerge from *I. obsoleta*, metacercariae of *L. setiferoides* do not simply encyst within their second-intermediate hosts, but continue to grow and develop for several weeks (Martin, 1938; McCurdy, pers. obs.). Thus, the costs of parasitism to the energy budgets of polychaete hosts are expected to increase over time after infection.

### Predictions

If *Pygospio elegans* responds to parasitism through life-history variation, I predicted that polychaetes would fragment soon after infection, before parasitism becomes costly. *P. elegans* also exhibits flexibility in asexual reproduction, as individual polychaetes may fragment into more than five pieces (Rasmussen, 1953; Gibson and Harvey, 2000). In light of this fact, I also expected that newly infected polychaetes might minimize the impacts of parasitism by isolating infection in small fragments or even lose infections by dividing across infected segments. In addition, *P. elegans* may also reproduce sexually (including poecilogonous development, with planktotrophic and adelophagic

larvae; Morgan *et al.*, 1999), so I examined polychaetes for evidence of sexual reproduction as a possible response to parasitism. For infected polychaetes, the advantages of sexual reproduction might include enhanced dispersal of offspring (Chia *et al.*, 1996)—possibly away from infected snails—and increased genetic variation (Lively, 1996). In fact, the evolution and maintenance of sexual reproduction have been explained as a host response to parasitism because sex is more likely to produce individuals that are able to escape parasitism over evolutionary timescales (reviewed by Hurst and Peck, 1996).

In addition to investigating host responses to parasitism, I assessed the impact of parasitism by *Lepocreadium setiferoides* on the asexual reproductive success of *P. elegans* over an 8-week period. I also assessed the costs of parasitism to survivorship and regeneration of polychaetes that had previously been cut into two fragments, mimicking the fragmentation that results from asexual reproduction or sublethal predation (Woodin, 1982; Zajac, 1995). In all cases, I considered two additional possibilities, other than adaptive host response, to explain observed changes in host behavior and development in relation to parasitism. First, such changes might have been due to adaptations of parasites to increase transmission rates (parasite manipulation; Poulin *et al.*, 1994). This possibility is particularly relevant to the parasite-host system I studied because there is evidence for parasite manipulation by cercariae and metacercariae of another trematode that parasitizes *Ilyanassa obsoleta* (Curtis, 1987; McCurdy *et al.*, 1999, 2000a). Second, observed changes in behavior might have been due to side effects of infection that are not adaptive for the host or parasite (Poulin, 1995).

## Materials and Methods

### Collections and infection protocols

I collected specimens of *Pygospio elegans* from a mudflat between Wyer and Orr's Islands, Harpswell, Maine (43°47'N, 69°58'W). This mudflat is located in Casco Bay, Gulf of Maine, and has semidiurnal tides that range from 2 to 4 m (Born, 1999). I chose to sample at the Wyer-Orr's mudflat because densities of *P. elegans* were high there (>20,000 m<sup>-2</sup>), but *Ilyanassa obsoleta* and its associated cercarial parasites were rare (<0.25 snails m<sup>-2</sup>), minimizing the likelihood that polychaetes used in experiments were already infected. I collected polychaete tubes in the mid-intertidal zone by sieving the top 5 cm of mud (500- $\mu$ m mesh) and transported tubes to the nearby running-seawater laboratory at the Coastal Studies Center of Bowdoin College for sorting. I retained only undamaged, entire adult polychaetes (>2 mm) that were not about to fragment (detectable because *P. elegans* constricts just prior to fission; Gibson and Harvey, 2000).

To obtain cercarial trematodes for experiments, I col-

lected specimens of *I. obsoleta* from throughout the intertidal zone at Strawberry Creek, Great Island, Maine (43°49'N, 69°58'W). This mudflat is located 2.5 km from the Wyer-Orr's mudflat and supports high densities of *I. obsoleta* ( $>10 \text{ m}^{-2}$ ). In the laboratory, I housed 550 mud snails in separate 9-oz plastic cups with 125 ml of filtered seawater (55  $\mu\text{m}$ , 31 ppt, 23 °C). I retained only large snails ( $>15 \text{ mm}$ , tip of apex to lip of siphonal canal) because previous studies have shown that the prevalence of *Leporecreadium setiferoides* increases with shell height of snails (Curtis, 1997; McCurdy *et al.*, 2000c). After 30 h, I examined each cup for cercariae of *L. setiferoides* (identified using McDermott, 1951), combined cercarial-infested seawater from cups of six snails that had shed cercariae, and pipetted 20 ml of the solution into each dish that contained a polychaete that was to be exposed. Unexposed polychaetes each received 20 ml of seawater from six cups that contained snails that did not shed cercariae (confirmed by dissection, as cercarial release is a poor indicator of infection status; Curtis and Hubbard, 1990).

### Experiments

To investigate the impact of parasites on the timing of asexual reproduction, I individually housed 52 adult specimens of *P. elegans* in 150-ml custard dishes filled with unfiltered seawater with or without cercariae (18 °C, 16 h light day<sup>-1</sup>). After 24 h, I transferred each polychaete to a new dish filled with seawater and lined with defaunated mud (prepared by passing mud through a 425- $\mu\text{m}$  sieve and heating it to 70 °C). Every 24 h, I suspended each dish from a harness and determined the status of each polychaete by observing its tube (or tubes) through the bottom of its dish with the aid of a fiber-optic illuminator and 10 $\times$  magnifying loupe. Polychaetes could easily be observed because they constructed tubes that opened against the bottoms of their dishes. Polychaetes were fed the pea-flower-based supplement Liquifry Marine (Interpet Inc.; Brown *et al.*, 1999) every 3 days (concentration = 1 drop l<sup>-1</sup>) following a complete change of water. I removed polychaetes from the experiment when they died or fragmented, and I measured the relaxed length of all fragments with an ocular micrometer (nearest 0.1 mm; Gudmundsson, 1985). I then dissected each fragment to determine if it was infected by trematode metacercariae and compared median time-to-fragmentation among exposed but uninfected, exposed and infected, and unexposed polychaetes. In making this comparison, I separated exposed but uninfected polychaetes from unexposed ones because of the possibility that host response might be associated with indirect cues associated with parasitism (*i.e.*, response might not require an actual infection to occur). To compare time-to-fragmentation, I applied a non-parametric Kruskal-Wallis ANOVA because the residuals

for all groups were non-normal. I then applied Dunn's method to compare differences among medians (Zar, 1996).

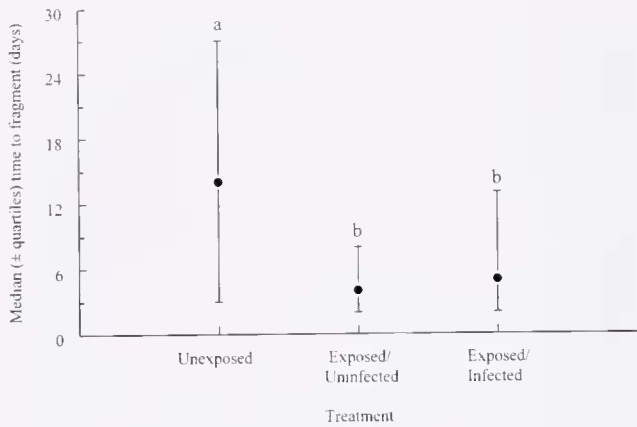
To investigate how exposure to parasites affected the reproductive success of *P. elegans*, I randomly housed 18 sets of 10 polychaetes (hereafter referred to as populations of polychaetes) in separate dishes and exposed half of the sets to cercariae of trematodes (housing conditions for polychaetes were as described above). Because the infection status of polychaetes that died during this experiment could not be determined without disturbing surviving polychaetes, I assessed rates of experimental and background infection by randomly removing two sentinel populations after 3 days: a population of polychaetes that had been exposed to cercariae, and a population of unexposed polychaetes. Rates of infection at that time represented maximum levels that could occur because cercariae of *L. setiferoides* survive for less than 48 h outside a host (Stunkard, 1972). After 8 weeks, I removed the remaining dishes and processed each population by counting the number of polychaetes retained after sieving (425- $\mu\text{m}$  mesh) and dissecting each polychaete to determine its infection status.

To assess survivorship and regenerative ability of newly divided polychaetes in relation to parasitism, I cut 59 polychaetes into two fragments and exposed 30 pairs of fragments to cercariae. Cutting each polychaete resulted in a smooth, clean blastema similar to that resulting from sublethal predation or asexual fragmentation (Gibson and Harvey, 2000; pers. obs.). To mimic conditions in nature, where newly fragmented polychaetes generally remain in the same burrow during regeneration (Gudmundsson, 1985; Gibson and Harvey, 2000), I individually housed original head and tail fragments together in a dish with seawater and mud (housing conditions as described above). To avoid disturbing fragments (as above), I assessed initial rates of infection at 3 days after exposure or non-exposure by removing and dissecting randomly chosen sentinel pairs of exposed fragments ( $n = 10$  polychaetes) and unexposed fragments ( $n = 10$  polychaetes). At 10 days after exposure or non-exposure, I removed all remaining fragments, measured their lengths, and determined their infection status.

## Results

### Parasitism and host fragmentation

In the experiment investigating the impact of trematodes on the timing of asexual reproduction in *Pygospio elegans*, parasite prevalence was low (42.3% of polychaetes exposed became infected;  $n = 26$ ). Asexual fragmentation always yielded two fragments; one containing the original head and thorax and a second containing the original tail (see Gibson and Harvey, 2000, for a description of body components). In all cases, polychaetes fragmented within 24 h of observable constrictions. Time-to-fragmentation differed between exposed and infected, exposed but uninfected, and unexposed



**Figure 1.** Median ( $\pm$  quartiles) numbers of days for asexual reproduction to occur in individuals of *Pygospio elegans* that were experimentally infected, exposed but not infected, and not exposed to cercariae of the trematode *Lepocreadium setiferoides*. Polychaetes and parasites were collected from mudflats in Harpswell, Maine, and housed in the laboratory. Medians with the same letter do not differ significantly from each other.

polychaetes ( $H_{(2,52)} = 10.56$ ,  $P < 0.01$ ; Fig. 1). Specifically, polychaetes that were exposed to cercariae but did not become infected fragmented earlier than unexposed polychaetes ( $Q = 2.99$ ,  $P < 0.005$ ), as did polychaetes that were exposed and became infected ( $Q = 2.16$ ,  $P < 0.05$ ). Of all polychaetes that were exposed to cercariae, however, infection status did not affect time-to-fragmentation ( $Q = 0.49$ , NS).

For unexposed polychaetes and exposed polychaetes that remained uninfected, fragments that contained original heads were larger than those that contained original tails, whereas lengths of original head and tail fragments did not differ for infected polychaetes (Table 1). In infected polychaetes, parasites were just as likely to be found in fragments that contained original heads ( $n = 5$ ) as those that contained original tails ( $n = 5$ ) (an additional polychaete harbored a metacercaria in each new fragment). For infected polychaetes, infected fragments were significantly larger than uninfected fragments (infected fragments:  $\bar{x} \pm s = 2.0 \pm 0.2$  mm; uninfected fragments:  $\bar{x} \pm s = 1.4 \pm 0.2$  mm; paired  $t_{(9)} = 2.28$ ,  $P < 0.05$ ), and in 9 of 10 cases, metacercariae were found in the larger fragment ( $X^2_{(1)} = 6.4$ ,  $P = 0.01$ ). Cercariae were not observed to penetrate segments that comprised, or were adjacent to, planes of fission.

#### Parasitism and host asexual reproductive success

At 3 days post exposure, 17 of 20 fragments (8.5 of the original 10 polychaetes) were alive in the sentinel population that was exposed to cercariae. Only one fragment in this population was infected by trematodes—a living tail fragment infected with a single metacercaria. In the sentinel population that was not exposed to cercariae, 18 of 20

fragments were alive after 3 days and no parasites were found (one fragment, containing an original head, was lost during processing). At 8 weeks after exposure or non-exposure, I saw no evidence of recent fission in polychaetes as all fragments had complete or nearly complete heads and tails. Therefore, I considered all fragments equally when measuring population sizes at that time. Populations of polychaetes that were exposed to cercariae were smaller than those that were not exposed (exposed populations:  $\bar{x} \pm s = 17.3 \pm 2.4$  polychaetes; unexposed populations:  $\bar{x} \pm s = 29.8 \pm 3.7$  polychaetes;  $t_{(14)} = 2.84$ ,  $P = 0.01$ ). When dissected, only seven polychaetes in exposed populations were infected (one polychaete in each of three populations and two polychaetes in each of two populations), and none of the polychaetes in any of the unexposed populations was infected.

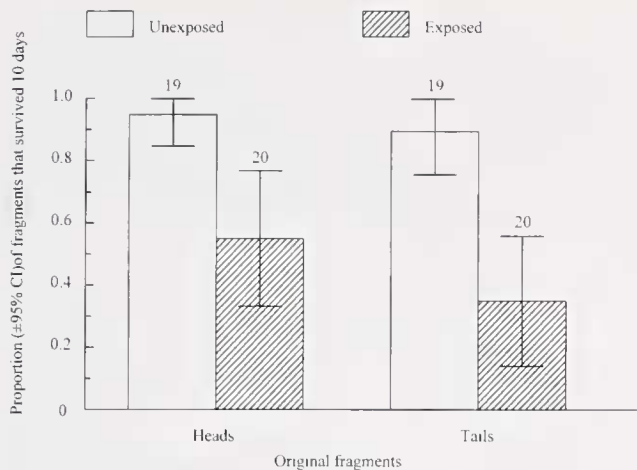
Considering sentinel polychaetes that had been cut into two pieces, 2 of 10 polychaetes exposed to cercariae were infected at 3 days post-exposure. In each case, the infection was in the original head fragment and by a single metacercaria. None of the 10 unexposed polychaetes was infected. When examining the remaining polychaetes 7 days later, I found that both head and tail fragments of exposed polychaetes were less likely to be alive than the respective fragments of unexposed polychaetes (head fragments:  $X^2_{(1)} = 8.07$ ,  $P < 0.005$ ; tail fragments:  $X^2_{(1)} = 12.22$ ,  $P < 0.001$ ; Fig. 2). Only two exposed polychaetes were infected by metacercariae (one polychaete had an infected tail fragment and another an infected head fragment;  $n = 20$ ), and no unexposed polychaetes were infected ( $n = 19$ ). In all cases, regeneration of "lost" components was nearly complete by 10 days, and lengths of original head and tail fragments did not differ in relation to exposure (unexposed heads:  $\bar{x} \pm SE = 2.65 \pm 0.15$ ; exposed heads:  $\bar{x} \pm SE = 2.56 \pm 0.26$ ;  $t_{(26)} = 0.32$ , NS; unexposed tails:  $\bar{x} \pm SE =$

**Table 1**

Sizes of fragments produced by asexual fission of *Pygospio elegans* in relation to parasitism

	Fragment length (mm)		Paired $t$ test
	Heads	Tails	
Unexposed	2.1 $\pm$ 0.2	1.57 $\pm$ 0.1	$t_{(23)} = 2.7$ , $P = 0.01$
Exposed but uninfected	2.4 $\pm$ 0.2	1.57 $\pm$ 0.2	$t_{(14)} = 2.3$ , $P = 0.04$
Exposed and infected	1.9 $\pm$ 0.2	1.71 $\pm$ 0.2	$t_{(10)} = 0.8$ , $P = 0.44$

Data are means and standard errors for lengths of fragments containing original heads and those containing original tails of polychaetes that were experimentally infected, exposed but not infected, and not exposed to cercariae of the trematode *Lepocreadium setiferoides*. The last column shows results from paired  $t$  tests for lengths of original head versus tail fragments.



**Figure 2.** Proportions ( $\pm 95\%$  confidence intervals) of original head and tail fragments of individuals of *Pygospio elegans* that survived for 10 days in the laboratory following exposure or non-exposure to cercariae of the trematode *Lepocreadium setiferoides*. Sample sizes are shown above the bars.

$2.71 \pm 0.19$ ; exposed tails:  $\bar{x} \pm SE = 2.49 \pm 0.28$ ;  $t_{(22)} = 0.63$ , NS).

## Discussion

### Parasitism and host fragmentation

In support of the hypothesis of adaptive host response I found that specimens of *Pygospio elegans* infected by metacercariae of *Lepocreadium setiferoides* hastened their onset of asexual reproduction relative to unexposed controls. By doing so, polychaetes may be expected to achieve greater reproductive success than if they had failed to respond because of increasing costs associated with parasitism over time (Forbes, 1993). However, my observation that early fragmentation also occurred in exposed polychaetes that remained uninfected complicates this interpretation. In a study that separated hosts by exposure and infection status, Minchella and Loverde (1981) found that freshwater snails of the species *Biomphalaria glabrata* increased their rates of early egg laying when infected by *Schistosoma mansoni*, but that the rates for exposed but uninfected individuals and unexposed controls did not differ. These authors argued that only infected snails responded because successful parasitism was associated with a high cost to future reproduction (castration).

For individuals of *P. elegans* exposed to, but not infected by, cercariae, early reproduction could still be an adaptive host response if exposure to cercariae in nature is a reliable indicator that costly infections will soon result (Minchella, 1985). Support for this idea comes from the observation that *Ilyanassa obsoleta* infected by *L. setiferoides*, although uncommon across mudflats, can remain for several months in small patches where some *P. elegans* are found (Mc-

Curdy *et al.*, 2000c). As a result, thousands of cercariae are shed in areas where infections are most likely to occur. Additional information on the infection process of *L. setiferoides* is necessary to determine whether polychaetes detect cercariae, and whether the exposure-related response resulted from the presence of cercariae or from failed attempts at penetration. There is evidence from other parasite-host systems that invertebrates can detect and exhibit anti-parasite behaviors to minimize the likelihood of infection (*e.g.*, Léonard *et al.*, 1999).

Early fragmentation of *P. elegans* is unlikely to be a parasite adaptation, because it apparently does not increase transmission rates for cercariae or metacercariae. Specifically, fragmentation was not associated with increased susceptibility to parasitism: most polychaetes fragmented after free-living cercariae would have ( $\geq 48$  h; Stunkard, 1972). For metacercariae, residing in small fragments would not appear to benefit transmission to final hosts, because flounder select prey at larger sizes relative to conspecifics, and even small differences in prey size preference can profoundly influence the energy budgets of predators foraging on mudflats (MacDonald and Green, 1986; Boates and Smith, 1989; Keats, 1990). To assess whether early fragmentation is actually adaptive for parasites or hosts, the consequences of early fragmentation could be further explored by constructing a model derived from empirical observations of parasites, their intermediate hosts, and the predators that are their final hosts. This approach was used recently to show that the early onset of receptivity to mating observed in females of the amphipod *Corophium volutator* infected by the trematode *Gynaecotyla adunca* resulted in greater reproductive success for the amphipods than if they had waited to become receptive at the optimal time for uninfected females (McCurdy *et al.*, 2001).

I found no evidence that fragmentation of *P. elegans* served to isolate or remove metacercariae, in that fission produced only two fragments, the smaller of which almost never contained metacercariae. It is unclear whether the greater presence of metacercariae in larger fragments is adaptive for the parasite or its host or whether larger fragments merely represent larger targets for parasites. Metacercariae might benefit from residing in larger fragments because of the availability of additional resources for parasite development or the possibility of a greater transmission rate to final hosts (as stated above, flounder tend to select larger prey). If residing in larger fragments is parasite-mediated, the observation that metacercariae develop near the site of initial penetration (Stunkard, 1972; pers. obs) indicates that the mechanism does not involve movements by metacercariae through the host coelom and into larger fragments. Fragmentation could also be interpreted as a host response: If larger fragments are better able to tolerate stresses associated with parasitism, the result would be a net reproductive benefit to hosts. In fact, host response need not

be exclusive of benefits to parasites, depending on the timing of altered behavior of infected hosts (McCurdy *et al.*, 1999). Simulated parasites such as Sephadex beads (Suwan-chaichinda and Paskewitz, 1998) could be used to help separate effects mediated by the parasite from those mediated by the host. Experiments with simulated parasites would provide cues to the host that it has become infected while removing the possibility of parasite manipulation.

Across all experiments, I found no evidence for onset of sexual reproduction, observing neither eggs nor spermatozoa. Seasonal constraints may have precluded sexual reproduction, which usually occurs only during the winter in *P. elegans* (Rasmussen, 1953; Gudmundsson, 1985; Wilson, 1985). However, even if the polychaetes had shown evidence of sexual reproduction, this tactic might be expected to increase reproductive success only if mates were available; an unlikely event given the rarity of parasites in natural populations of *P. elegans* (above).

#### *Parasitism and host asexual reproductive success*

I found that even a low level of exposure to cercariae (on average, 8% of cercariae that a single snail sheds in 30 h) reduced the asexual reproductive success of *P. elegans* (45%, measured in populations 8 weeks after exposure). In a related finding from another experiment, both head and tail fragments were less likely to survive to complete regeneration than were unexposed fragments. Direct effects of parasitism are not sufficient to account for these results given that few exposed polychaetes actually became infected in either experiment. One possibility is to explain the reduced reproductive success of exposed but uninfected hosts as the result of a trade-off between host reproductive effort and costly activities associated with defenses against parasites. Recent work has shown that hosts exposed to parasites may trade off energy used in reproduction for behaviors or immune responses to resist parasites (Sheldon and Verhulst, 1996; Léonard *et al.*, 1999).

Regardless of the underlying causes, the dramatic reduction in reproductive success of *P. elegans* after exposure to cercariae has implications for natural populations of this species and for soft-bottom intertidal communities. *Pygospio elegans* often dominates such communities, and thus can directly affect the distribution and abundance of other infauna (Wilson, 1983; Brey, 1991; Kube and Powilleit, 1997). In addition, it is possible that parasitism of *P. elegans* may influence the structure of intertidal communities by altering or creating engineering functions in hosts. Engineering functions are those that produce new habitat as a result of changes in behaviors or life history associated with parasitism (Thomas *et al.*, 1999). Clearly, researchers should consider the impacts of parasites on the ecology and evolution of the reproductive strategies of marine invertebrates and on the structure of infaunal communities.

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